Earliest known Oldowan artifacts at >2.58 Ma from Ledi-Geraru, Ethiopia, highlight early technological diversity

David R. Braun[a,b,1], Vera Aldeias[b,c], Will Archer[b,d], J Ramon Arrowsmith[e], Niguss Baraki[f], Christopher J. Campisano[g], Alan L. Deino[h], Erin N. DiMaggio[i], Guillaume Dupont-Nivet[j,k], Blade Engda[l], David A. Feary[e], Dominique I. Garello[e], Zenash Kerfelew[l], Shannon P. McPherron[b], David B. Patterson[a,m], Jonathan S. Reeves[a], Jessica C. Thompson[n], and Kaye E. Reed[g]

[a]Center for the Advanced Study of Human Paleobiology, Department of Anthropology, The George Washington University, Washington DC 20052; [b]Department of Human Evolution, Max Planck Institute of Evolutionary Anthropology, 04103 Leipzig, Germany; [c]Interdisciplinary Center for Archaeology and the Evolution of Human Behaviour, University of Algarve, Campus de Gambelas, 8005-139 Faro, Portugal; [d]Archaeology Department, University of Cape Town, 7701 Rondebosch, South Africa; [e]School of Earth and Space Exploration, Arizona State University, Tempe, AZ 85287; [f]Department of Archaeology and Heritage Management, Main Campus, Addis Ababa University, Addis Ababa, Ethiopia; [g]Institute of Human Origins, School of Human Evolution and Social Change, Arizona State University, Tempe, AZ 85287; [h]Berkeley Geochronology Center, Berkeley, CA 94709; [i]Department of Geosciences, Pennsylvania State University, University Park, PA 16802; [j]CNRS, Géosciences Rennes–UMR 6118, University of Rennes, F-35000 Rennes, France; [k]Department of Earth and Environmental Science, Postdam University, 14476 Potsdam-Golm, Germany; [l]Authority for Research and Conservation of Cultural Heritage, Addis Ababa, Ethiopia; [m]Department of Biology, University of North Georgia, Dahlonega, GA 30533; and [n]Department of Anthropology, Yale University, New Haven, CT 06511

Edited by James F. O'Connell, University of Utah, Salt Lake City, UT, and approved April 5, 2019 (received for review November 26, 2018)

The manufacture of flaked stone artifacts represents a major milestone in the technology of the human lineage. Although the earliest production of primitive stone tools, predating the genus *Homo* and emphasizing percussive activities, has been reported at 3.3 million years ago (Ma) from Lomekwi, Kenya, the systematic production of sharp-edged stone tools is unknown before the 2.58–2.55 Ma Oldowan assemblages from Gona, Ethiopia. The organized production of Oldowan stone artifacts is part of a suite of characteristics that is often associated with the adaptive grade shift linked to the genus *Homo*. Recent discoveries from Ledi-Geraru (LG), Ethiopia, place the first occurrence of *Homo* ∼250 thousand years earlier than the Oldowan at Gona. Here, we describe a substantial assemblage of systematically flaked stone tools excavated in situ from a stratigraphically constrained context [Bokol Dora 1, (BD 1) hereafter] at LG bracketed between 2.61 and 2.58 Ma. Although perhaps more primitive in some respects, quantitative analysis suggests the BD 1 assemblage fits more closely with the variability previously described for the Oldowan than with the earlier Lomekwian or with stone tools produced by modern nonhuman primates. These differences suggest that hominin technology is distinctly different from generalized tool use that may be a shared feature of much of the primate lineage. The BD 1 assemblage, near the origin of our genus, provides a link between behavioral adaptations—in the form of flaked stone artifacts—and the biological evolution of our ancestors.

Oldowan | stone tools | *Homo* | cultural evolution | paleoanthropology

Stone artifacts represent the most enduring evidence of early human behavior. As such, the archaeological record is uniquely suited to investigate the evolution of behavior in our lineage (1). For much of the study of the Paleolithic, the Oldowan has represented the origin of human tool use (2, 3) and a hallmark of hominin cognitive capabilities (4). Recent studies, however, have highlighted the extent of nonhuman primate tool use (5, 6) as well as the evidence for more ancient forms of hominin tool use (7, 8). Here, we present an Oldowan assemblage that predates the currently known oldest stone artifacts from Gona, Ethiopia. An analysis of Early Stone Age technologies suggests that the Oldowan is a technologically distinct change from the generalized pattern of tool use that is employed by many primates.

Results

The LG Research Project (LGRP) area is in the lower Awash Valley (LAV), Ethiopia (Fig. 1). The LGRP area contains sedimentary strata that overlie the Hadar (∼3.8–2.9 Ma) and underlie the Busidima (∼2.7–0.16 Ma) Formations (9), representing an interval that is poorly known from the LAV specifically and in eastern Africa generally. Paleoenvironmental and geological analyses have documented a more open habitat than previously recognized in the LAV (9) in association with the LD 350–1 mandible, the earliest hominin fossil with derived mandibular features that define the genus *Homo* (10).

In 2012, at the BD 1 locality in the eastern LGRP area, a number of stone artifacts were identified embedded in a steep west-facing slope adjacent to the Korkora basalt horst in the Ali Toyta river drainage (Fig. 2). BD 1 is ∼5 km north of the Lee Adoyta region where the LD 350–1 mandible was recovered in 2013 (10). The LGRP excavated 37 m^2 at BD 1 at an average depth of 1.8 m below surface during field seasons in 2013 and

Significance

Humans are distinguished from all other primates by their reliance on tool use. When this uniquely human feature began is debated. Evidence of tool use in human ancestors now extends almost 3.3 Ma and becomes prevalent only after 2.6 Ma with the Oldowan. Here, we report a new Oldowan locality (BD 1) that dates prior to 2.6 Ma. These earliest Oldowan tools are distinctive from the 3.3 Ma assemblage and from materials that modern nonhuman primates produce. So, although tool production and use represent a generalized trait of many primates, including human ancestors, the production of Oldowan stone artifacts appears to mark a systematic shift in tool manufacture that occurs at a time of major environmental changes.

Author contributions: D.R.B., V.A., W.A., J.R.A., N.B., C.J.C., A.L.D., E.N.D., G.D.-N., B.E., D.A.F., D.I.G., Z.K., S.P.M., D.B.P., J.S.R., J.C.T., and K.E.R. designed research; D.R.B., V.A., W.A., J.R.A., N.B., C.J.C., A.L.D., E.N.D., G.D.-N., B.E., D.A.F., D.I.G., Z.K., S.P.M., D.B.P., J.S.R., J.C.T., and K.E.R. performed research; N.B., C.J.C., A.L.D., E.N.D., G.D.-N., B.E., D.A.F., D.I.G., S.P.M., D.B.P., J.S.R., and K.E.R. contributed new reagents/analytic tools; D.R.B., V.A., W.A., J.R.A., N.B., A.L.D., E.N.D., G.D.-N., B.E., D.A.F., D.I.G., S.P.M., D.B.P., J.S.R., J.C.T., and K.E.R. analyzed data; and D.R.B., V.A., W.A., J.R.A., N.B., C.J.C., A.L.D., E.N.D., G.D.-N., B.E., S.P.M., J.C.T., and K.E.R. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

[1]To whom correspondence should be addressed. Email: david_braun@gwu.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1820177116/-/DCSupplemental.

The bed overlying the archaeological horizon rapidly grades laterally (~3 m westward) from a clayey-silt with mollusk (gastropod and bivalve) shells to a pebble conglomerate. The underlying clay horizon contains dispersed gastropod shells and displays vertic structure and development of gilgai microrelief. Micromorphological evidence indicates the presence of a relatively stable land surface upon which the artifacts were deposited (*SI Appendix*, Figs. S1–S3).

The Ali Toyta sedimentary package reflects several phases of lacustrine and perilacustrine deposition followed by subaerial exposure and pedogenic development. The BD 1 archaeological horizon formed on a surface of exposed lacustrine clays following a lake regression with sufficient subaerial exposure to allow for vertisol development. The site was subsequently buried and possibly reworked by low energy sheet flow during a later transgressive phase of the lake that deposited coarser grained material as well as gastropods and bivalves, likely representing a beach or nearshore deposit (Fig. 3 and *SI Appendix*, Figs. S3 and S4).

Site formation analysis (fabric analysis; *SI Appendix*, Fig. S5*A*) and soil micromorphological observations indicate that the artifacts at BD 1 were deposited on an exposed clay surface. The combined presence of small artifacts (<2 cm) and fragile microfossils, the lack of artifact rounding, find orientations (*SI Appendix*, Fig. S5*A*), and differences in the spatial distribution of artifacts relative to nonartifactual stones (*SI Appendix*, Fig. S6) all indicate that the material was not subjected to extensive postdepositional disturbance. Relatively minor artifact reworking subsequent to deposition is suggested by the lower frequency of the smallest fraction of artifacts (<2 cm) compared with experimental studies (*SI Appendix*, Fig. S5*B*). Several faunal specimens (25.2% of the assemblage) exhibit substantial smoothing and rounding, suggesting that some of the fauna are allochthonous. The stratigraphically discrete nature of the archaeological horizon is further supported by a high correlation between the variation

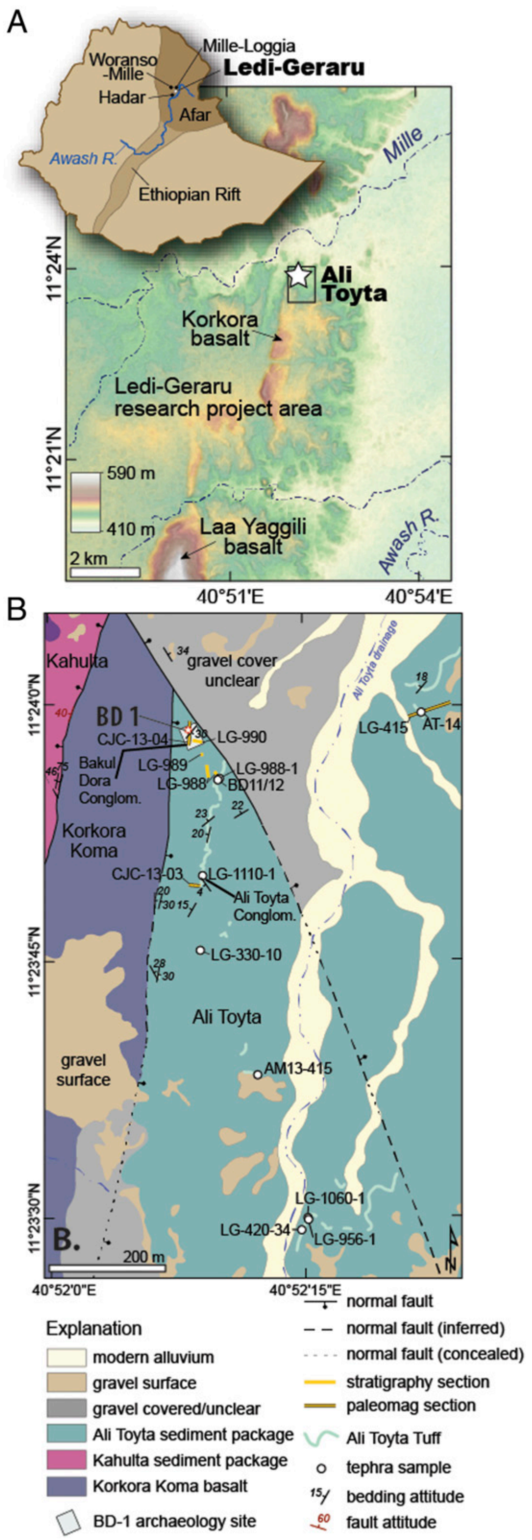

Fig. 1. Location of BD 1: (*A*) Location of the eastern LG research area in Ethiopia and within the Afar Depression. (*B*) Geological map of the Ali Toyta fault block region.

2015. During this excavation, 300 stone artifacts and 330 associated fossils were recovered in situ (*SI Appendix*, Table S1) from within a restricted stratigraphic interval at the interface of two distinct sedimentary units (76% of the assemblage comes from a 4–12 cm thick horizon) (Fig. 3).

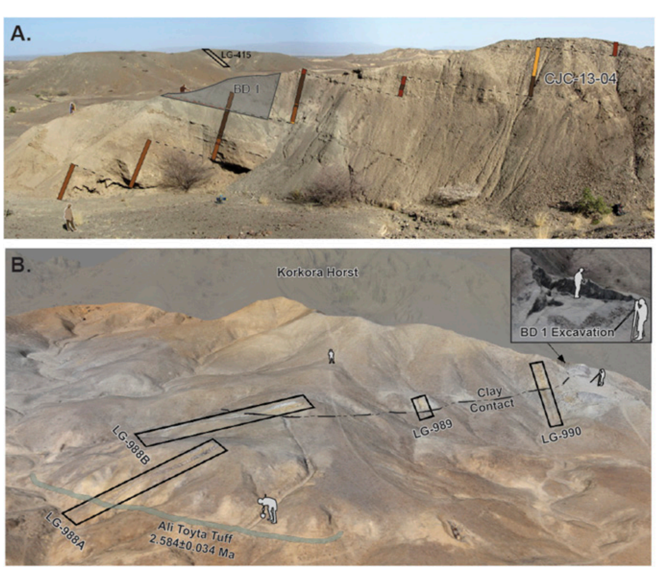

Fig. 2. Aerial views. (*A*) The archaeological site of BD 1 (view toward the east-northeast). Overlain notations indicate the stratigraphic units (Fig. 3). This photograph was taken before excavations. The grayed out area represents the extent of excavations in 2015. (*B*) Oblique aerial perspective (west facing) of the high-resolution model of the BD 1 excavation site (*Inset*) within the broader local area; the model also shows the multiple trenches used to track geological horizons for linking BD 1 with the ~2.58 Ma Ali Toyta Tuff (LG-labeled trenches are shown as stratigraphic columns in *SI Appendix*, Fig. S3). Scale shown by figure silhouettes at different locations on the model images.

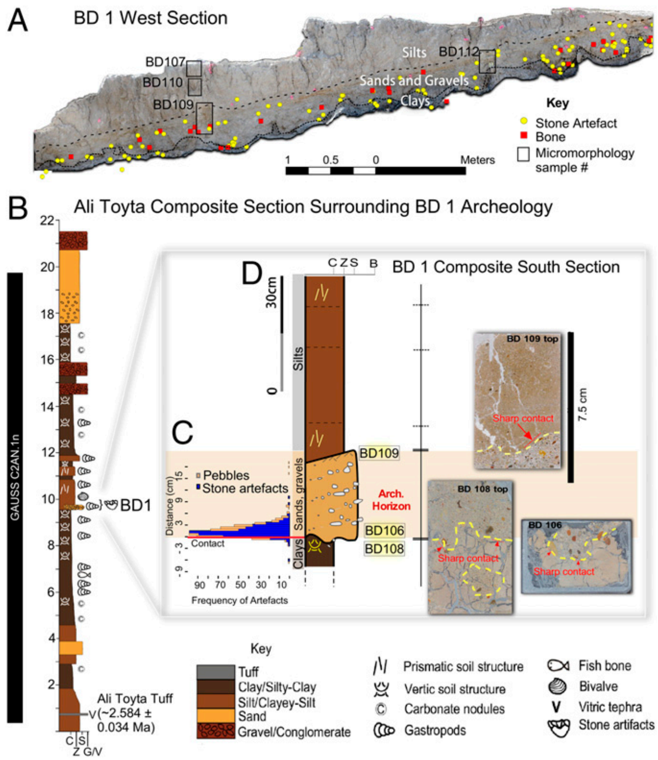

Fig. 3. Stratigraphic information on BD 1. (*A*) West wall section of BD 1 and associated artifacts. Specimens plotted represent westernmost excavation units (UTM Eastings 703932–703933). Black dashed lines on a section denote boundaries of stratigraphic units defined in *D* with the location of soil micromorphology samples shown. Note that the tilting of the stratigraphic units is due to postdepositional processes. (*B*) Stratigraphic column at BD 1. (*C*) Distribution of pebbles and artifacts relative to the sharp contact among clays, overlying sands, and gravel layer (red line). (*D*) Detailed stratigraphic column at BD 1 with soil micromorphology thin section scans of the archaeological horizon. The annotations on the scans highlight the sharp wavy contact between the two stratigraphic layers. Yellow numbered boxes refer to soil micromorphological sample locations (*SI Appendix*, Figs. S1–S3). Soil micromorphological samples BD106 and BD108 were collected along the south wall of the excavation and are not displayed in Fig. 3*A*.

in artifact elevation and that of the undulating elevation of the underlying clay horizon ($r^2 = 0.89$; $n = 1424$; SE: 4.49).

The age of the site is constrained by radioisotopic and magnetostratigraphic dating (Fig. 3 and *SI Appendix*, Fig. S3). The BD 1 archaeological horizon is 8.8 m stratigraphically above a 5–10 cm thick water-lain vitric tephra layer—the Ali Toyta Tuff—(*SI Appendix*, Table S2 and extended datasets S1 and S2) which yielded a $^{40}Ar/^{39}Ar$ age on K-feldspar phenocrysts of 2.584 ± 0.034 Ma (95% confidence estimate) (*SI Appendix*, Figs. S7–S9 and extended dataset S3). Paleomagnetic analyses of multiple sections at Ali Toyta from stratigraphically below the Ali Toyta Tuff to above the artifact horizon are all of normal polarity (Fig. 3 and *SI Appendix*, Figs. S9 and S10 and Table S3), which represent the upper Gauss Chron [C2An.1n, 3.032–2.581 Ma (11)]. Above this Chron, the reverse polarity Matuyama Chron has yet to be identified in the Ali Toyta drainage and may not be preserved. Therefore, the BD 1 assemblage was most likely deposited between the Ali Toyta Tuff (~2.61–2.58 Ma) and the Gauss-Matuyama reversal (2.581 Ma). We conservatively adopt an age of ~2.58 Ma for the assemblage noting, however, that it must be older than the Gauss-Matuyama reversal. This demonstrates that the BD 1 locality is older than previously documented Oldowan sites, all of which occur in the reverse polarity Matuyama Chron (2); (*SI Appendix*, Fig. S9). The age interval

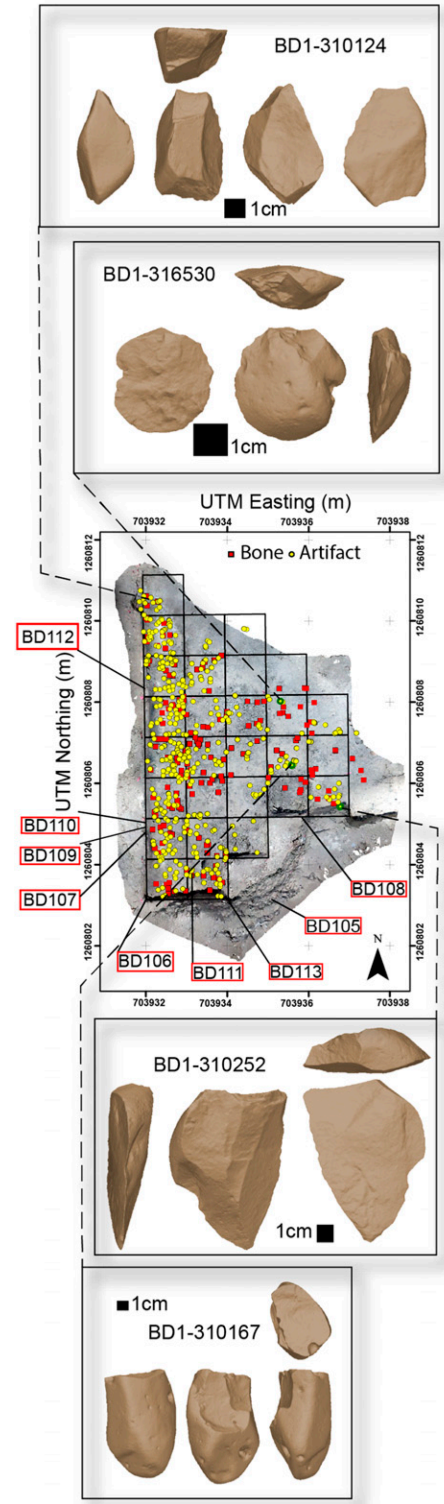

Fig. 4. Georectified 3D model of the BD 1 excavation surface. The black squares represent excavation units. Micromorphology sample locations are denoted by red boxes and corresponding sample name (*SI Appendix*, Figs. S1–S3 for further explanation). Selected artifacts are displayed as 3D models without surface texture to enhance features of conchoidal fracture (*SI Appendix*, Figs. S13 and S14 for images and *SI Appendix*, Table S6 for links to 3D models of artifacts).

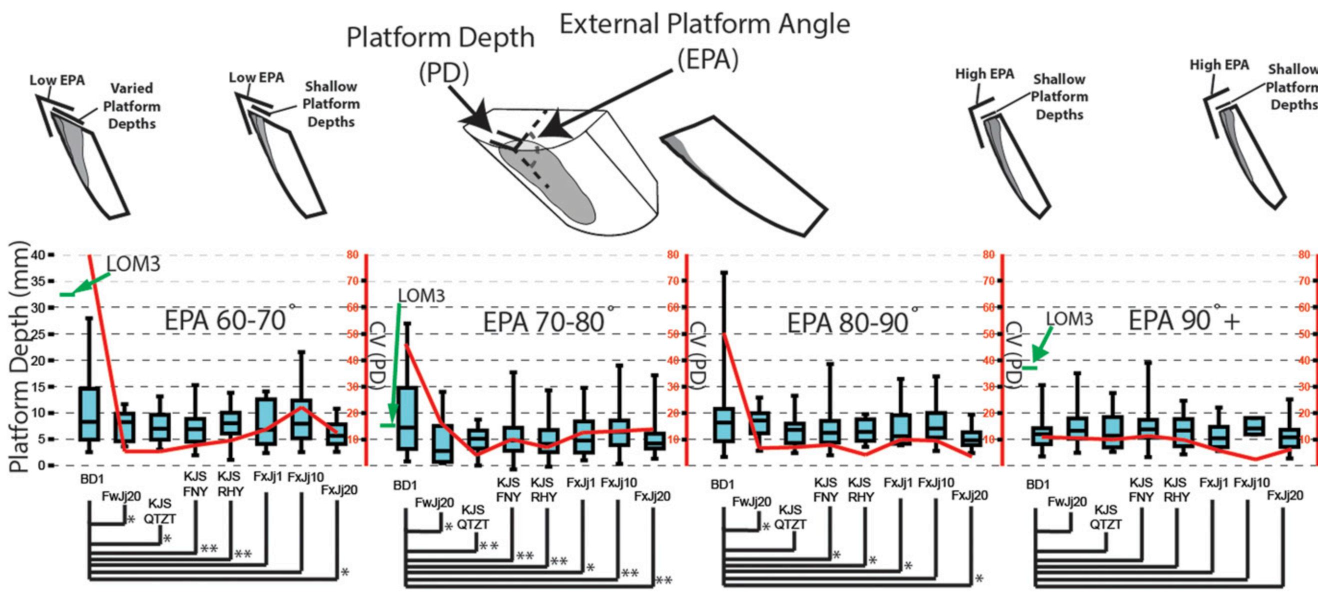

Fig. 5. Comparison of variation in platform depth within specific external platform angle intervals for BD 1 and several other Oldowan sites [Kanjera South (2.0 Ma); FxJj1-Koobi Fora (1.87 Ma); FxJj10-Koobi Fora (1.78 Ma); FxJj20-Koobi Fora (1.5 Ma); reprinted from ref. 18, with permission from Elsevier]. The BD 1 assemblage shows significantly greater variation than other Oldowan sites especially in the lower platform angle categories. Asterisks below the graph indicate levels of significance for an F test of variance between groups with Bonferroni correction for multiple tests. Note the lack of significance at the higher platform angle categories (>90°). At higher external platform angles, the amount of force required to initiate fracture increases exponentially with increases in platform depth (18) and likely places physical limits on the variation that can exist in this category. The green lines represent similar data from the three published flakes with visible platforms from Lomekwi 3 (LOM3) (LOM3-2012-H17-3; LOM3-2011-SURF-NW-7; LOM3-2012-J11-3).

encompassed by these strata overlaps that of other sedimentary packages in the eastern LGRP region, ranging from 2.99 to 2.45 Ma (9, 12).

The BD 1 faunal assemblage shares taxonomic similarities with the fauna from directly below the Gauss-Matuyama reversal in the Lee Adoyta fault block ∼5 km to the south (13). These assemblages indicate the proximity of open grassland in association with nearby lacustrine habitats (9) (*SI Appendix*, Table S4). This is consistent with previous studies that identified distinct environmental shifts relative to the earlier Hadar Formation (9). Only about half of the faunal specimens (53.4%) had 50% or more of the bone surface visible. This limited visibility makes it difficult to extract behavioral implications from bone surface modifications at BD 1 (*SI Appendix*, Fig. S11).

Artifacts from BD 1 show clear signs of conchoidal fracture including prominent bulbs of percussion, points of percussion, and contiguous flake scars on cores and on the dorsal surfaces of flakes (Fig. 4 and *SI Appendix*, Figs. S13 and S14 and Table S6). The majority of stone artifacts (64%) are made from a single type of fine-grained rhyolite that fractured predictably and has few internal flaws. Based on the occurrence of rhyolite pebbles and cobbles in conglomerate beds laterally continuous with the excavation horizon at BD 1, this material was readily available on the ancient landscape. Our analysis of these clasts (sampled up to 500 m from BD 1) shows that similar rock types are indeed present, but at lower frequencies, compared with their occurrence as artifacts in the BD 1 assemblage (*SI Appendix*, Figs. S3 and S12). The selection of specific rock types for artifact manufacture at BD 1 is also exhibited in later archaeological sites ranging from 2.5 to 1.78 Ma (14–16).

The BD 1 artifact assemblage is composed primarily of simple cores and flakes with smaller detached pieces (52%; <3 cm) being most abundant. The dominant flaking strategy was relatively simple with 45% of cores exhibiting flake scars on a single removal surface (*SI Appendix*, Fig. S14). Many flake scars end in step fractures (31%; *SI Appendix*, Fig. S15), which is consistent with many other Oldowan assemblages. Although flake scars on cores show clear indications of conchoidal fracture, most cores (62%) have only one or two flake scars (*SI Appendix*, Fig. S14). We identified no refits in this assemblage. Few artifacts show evidence of percussive activities that is not related to flaked stone tool manufacture (e.g., hammering or battering), and cores with multiple (>2) adjacent removals indicate some control of flaking (*SI Appendix*, Fig. S14). Core and flake sizes at BD 1 are similar to those found at younger Oldowan sites (*SI Appendix*, Fig. S16 and extended dataset S4). Quantitative technological analyses of the BD 1 artifacts indicate that hominins had not yet mastered the skills that experimental studies have shown to be critical in the systematic production of sharp edges [e.g., location of percussion, identifying optimal platforms; Fig. 5 (17–19)]. However, in many respects, the overall technological pattern of the BD 1 assemblage most closely aligns with that of the earliest Oldowan sites (Fig. 6 and *SI Appendix*, Figs. S15–S17 and Table S5). In particular, when the next oldest Oldowan site (OGS 7), BD 1, and LOM3 are compared along the attributes that show the most variability in the early Oldowan (>2.0 Ma), BD 1 is more similar to the oldest Oldowan assemblages and Lomekwi falls outside the range of variability for this time period (*SI Appendix*, Fig. S18) (20).

The older 3.3 Ma LOM3 assemblage represents a distinctive technology compared with BD 1 and other Oldowan sites (Fig. 6). LOM3 includes extraordinarily large cores with relatively few flaking surfaces and extensive evidence of battering associated with percussive activities (7) (*SI Appendix*, Fig. S15). Many Oldowan sites, including BD 1, have a higher frequency of small flakes with discrete platforms (*SI Appendix*, Fig. S15) and limited evidence of percussive actions (Fig. 6). These features indicate that Oldowan technology represents a distinct technological pattern. Whether this is evidence for an independent invention of the Oldowan will depend on whether additional sites showing directional change can be found in the still rather substantial interval between LOM3 and BD 1. For now, though, these data combined with the recent documentation of tool use among a variety of primate species (5, 6, 21), suggest an initially diverse and potentially convergent set of tool-assisted behavioral adaptations among early hominins (22).

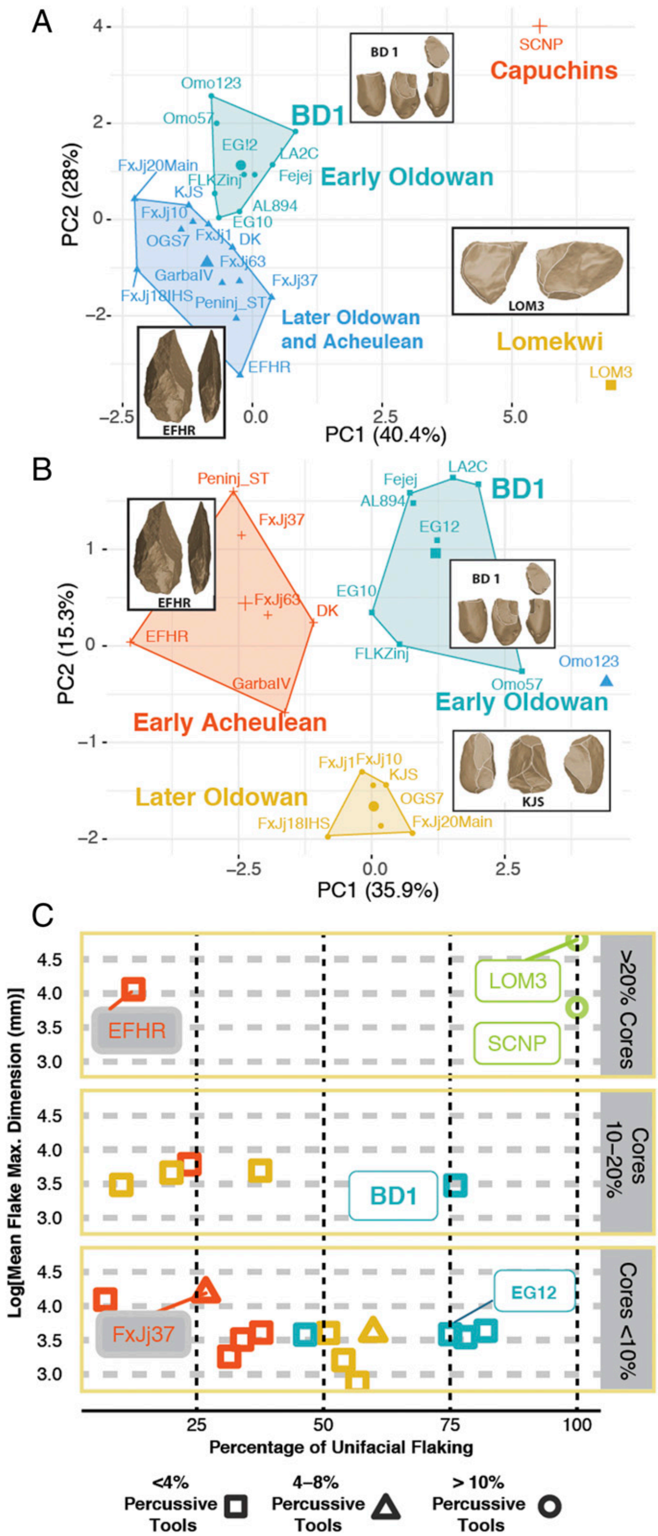

Fig. 6. (*A*) Principal components analysis (PCA) of major technological features of numerous Early Stone Age sites (*SI Appendix*, Table S8). The PCA scores were used to calculate a K-means cluster analysis. The shaded polygons (convex hulls) represent the results of the K-means cluster analysis. The analysis was conducted initially (*A*) including the Lomekwian site of LOM3 and the assemblages from Serra da Capivara National Park (SCNP), Brazil, made by capuchins in Brazil. (*B*) The same analyses were recalculated without the LOM3 and SCNP assemblages. The details of the PCA (*SI Appendix*, Fig. S17) and the details of the data selected for this analysis can be found in *SI Appendix*. (*C*) Analysis of several technological features of sites from the Pliocene and Early Pleistocene. Variables in this figure were chosen based on ordination techniques that indicate that these variables represent the greatest amount of variation in the data.

Discussion

The substantial assemblage of flaked stone artifacts from BD 1 marks the onset of hominin understanding of sequential flake removal and systematic flake production that is a characteristic of the Oldowan (Fig. 4 and *SI Appendix*, Figs. S13–S17 and Tables S7 and S8). In this regard, it is distinct from the much earlier LOM3 assemblage. LOM3, along with the contentious butchered bones from Dikika, Ethiopia (8), suggest that generalized tool use may be a shared ancestral trait of many hominins that is already present in the last common ancestor with *Pan*. This may be reflective of a more generalized primate pattern of tool use (7, 8, 23). Although the earliest stone tool use may have enhanced the extractive foraging abilities of members of the genus *Australopithecus* (24, 25), as it does in many living primates (26–28), the ability to systematically produce sharp-edged flakes at BD 1 constitutes a derived trait likely related to new foraging strategies (29). Systematic flake production would have dramatically increased the foraging return for resources that can be processed with sharp-edged tools (1, 30). This shift to a broader dietary adaptation may have resulted in a subsequent release of selective pressures on the earliest members of the genus *Homo* (31–33) and occurs concurrently with environmental shifts in northern Ethiopia (9, 13).

BD 1 is the oldest known Oldowan assemblage. Although it is a single assemblage, further discoveries are likely to expose greater diversity in Pliocene tool use. Despite its antiquity, however, the BD 1 assemblage, along with the early Oldowan, is technologically distinct from older Pliocene technology and from the tool use seen in modern nonhuman primates. The link between Oldowan technology and preceding technologies, or to any other potentially ancestral primate tool use strategy (1, 34), is currently unclear. Technological adaptations that are the hallmark of our genus, especially in the later Pleistocene (35), may be a derived feature with an independent origin relative to a series of diverse tool-assisted behaviors that began much earlier in the Pliocene (7, 8).

Methods

Excavation Procedures. All material was excavated according to discrete stratigraphic horizons and was mapped to the nearest millimeter using a total station Leica Builder 505 with a TDS Nomad 900 LE using EDM Mobile 5.1bt (36). Detailed stratigraphic information for many artifacts was captured using 3D photogrammetric models of artifacts in their in situ context.

Geological Methods. The age of BD 1 was determined using tephrostratigraphic, radiometric, and paleomagnetic techniques described in the *SI Appendix*. The context of the locality used a combination of soil micromorphological methods as well as site fabric analysis described in the *SI Appendix*.

Archaeological Methods. The stone artifact and fossil bones were analyzed using standardized procedures described in the *SI Appendix*. The study of the stone artifacts involved detailed comparison with numerous Oldowan and Acheulean assemblages that is described in the *SI Appendix*. Analysis of the associated fossil fauna included standard taphonomic and paleoecological methods.

ACKNOWLEDGMENTS. We thank the Authority for Research and Conservation of Cultural Heritage, Ethiopian Ministry of Culture and Tourism, for permission to conduct fieldwork at Ledi-Geraru and laboratory research in the National Museum of Ethiopia, Addis Ababa, where the BD 1 artifacts are housed. This research was sponsored by National Science Foundation Grants BCS-1460502, BCS-1157346, BCS-1460493, and BCS-1157351. This paper was made possible through the support of a grant from the John Templeton Foundation. The opinions expressed in this paper are those of the authors and do not necessarily reflect the views of the John Templeton Foundation.

1. Shea JJ (2017) Occasional, obligatory, and habitual stone tool use in hominin evolution. *Evol Anthropol* 26:200–217.
2. Semaw S, et al. (1997) 2.5-million-year-old stone tools from Gona, Ethiopia. *Nature* 385:333–336.
3. Leakey MD (1971) *Olduvai Gorge* (Cambridge Univ Press, Cambridge, UK).
4. Toth N, Schick K (2018) An overview of the cognitive implications of the Oldowan Industrial complex. *Azania* 53:3–39.
5. Haslam M, et al. (2009) Primate archaeology. *Nature* 460:339–344.
6. Proffitt T, et al. (2016) Wild monkeys flake stone tools. *Nature* 539:85–88.
7. Harmand S, et al. (2015) 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature* 521:310–315.
8. McPherron SP, et al. (2010) Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* 466:857–860.
9. DiMaggio EN, et al. (2015) Paleoanthropology. Late Pliocene fossiliferous sedimentary record and the environmental context of early Homo from Afar, Ethiopia. *Science* 347:1355–1359.
10. Villmoare B, et al. (2015) Paleoanthropology. Early Homo at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia. *Science* 347:1352–1355.
11. Gradstein FM, Ogg JG, Schmitz M, Ogg G (2012) *The Geologic Time Scale 2012* (Elsevier, Amsterdam, The Netherlands).
12. Dimaggio EN (2013) *The Geologic History of Central and Eastern Ledi-Geraru* (Afar, Ethiopia).
13. Robinson JR, Rowan J, Campisano CJ, Wynn JG, Reed KE (2017) Late Pliocene environmental change during the transition from Australopithecus to Homo. *Nat Ecol Evol* 1:159.
14. Stout D, Quade J, Semaw S, Rogers MJ, Levin NE (2005) Raw material selectivity of the earliest stone toolmakers at Gona, Afar, Ethiopia. *J Hum Evol* 48:365–380.
15. Harmand S (2009) Variability in raw material selectivity at the late Pliocene sites of Lokalalei, West Turkana, Kenya. *Interdisciplinary Approaches to the Oldowan*, eds Hovers E, Braun DR (Springer, Dordrecht, The Netherlands), pp 85–97.
16. Braun DR, et al. (2008) Oldowan behavior and raw material transport: Perspectives from the Kanjera formation. *J Archaeol Sci* 35:2329–2345.
17. Geribàs N, Mosquera M, Vergès JM (2010) What novice knappers have to learn to become expert stone toolmakers. *J Archaeol Sci* 37:2857–2870.
18. Dibble HL, Rezek Z (2009) Introducing a new experimental design for controlled studies of flake formation: Results for exterior platform angle, platform depth, angle of blow, velocity, and force. *J Archaeol Sci* 36:1945–1954.
19. Nonaka T, Bril B, Rein R (2010) How do stone knappers predict and control the outcome of flaking? Implications for understanding early stone tool technology. *J Hum Evol* 59:155–167.
20. Stout D, Semaw S, Rogers MJ, Cauche D (2010) Technological variation in the earliest Oldowan from Gona, Afar, Ethiopia. *J Hum Evol* 58:474–491.
21. Luncz LV, Mundry R, Boesch C (2012) Evidence for cultural differences between neighboring chimpanzee communities. *Curr Biol* 22:922–926.
22. Richerson PJ, Boyd R (2005) *Not by Genes Alone* (Univ of Chicago Press, Chicago).
23. Panger MA, Brooks AS, Richmond BG, Wood B (2002) Older than the Oldowan? Rethinking the emergence of hominin tool use. *Evol Anthropol* 11:235–245.
24. Teaford MF, Ungar PS (2000) Diet and the evolution of the earliest human ancestors. *Proc Natl Acad Sci USA* 97:13506–13511.
25. Thompson JC, Carvalho S, Marean CW, Alemseged Z (2019) Origins of the human predatory pattern: The transition to large-animal exploitation by early hominins. *Curr Anthropol* 60:1–23.
26. Sanz CM, Morgan DB (2013) Ecological and social correlates of chimpanzee tool use. *Philos Trans R Soc Lond B Biol Sci* 368:20120416.
27. Koops K, Visalberghi E, van Schaik CP (2014) The ecology of primate material culture. *Biol Lett* 10:20140508.
28. Spagnoletti N, et al. (2012) Stone tool use in wild bearded capuchin monkeys, Cebus libidinosus. Is it a strategy to overcome food scarcity? *Anim Behav* 83:1285–1294.
29. de Heinzelin J, et al. (1999) Environment and behavior of 2.5-million-year-old Bouri hominids. *Science* 284:625–629.
30. Zink KD, Lieberman DE (2016) Impact of meat and lower Palaeolithic food processing techniques on chewing in humans. *Nature* 531:500–503.
31. Laird MF, Vogel ER, Pontzer H (2016) Chewing efficiency and occlusal functional morphology in modern humans. *J Hum Evol* 93:1–11.
32. Ungar PS, Grine FE, Teaford MF (2006) Diet in early Homo: A review of the evidence and a new model of adaptive versatility. *Annu Rev Anthropol* 35:209–228.
33. Cerling TE, et al. (2013) Stable isotope-based diet reconstructions of Turkana Basin hominins. *Proc Natl Acad Sci USA* 110:10501–10506.
34. Tennie C, Premo LS, Braun DR, McPherron SP (2017) Early stone tools and cultural transmission: Resetting the null hypothesis. *Curr Anthropol* 58:652–654.
35. Marean CW, et al. (2007) Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. *Nature* 449:905–908.
36. McPherron SP, Dibble HL (2011) *Using Computers in Archaeology: A Practical Guide* (McGraw-Hill/Mayfield, Boston).